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THE VASCULAR ANATOMY OF CALAMOVILFA LONGIFOLIA.*

ERNEST LINCOLN STOVER

Eastern Illinois State Teachers' College

The present study of the anatomy of *Calamovilfa* was undertaken first because of the great difference observed between the mature vascular bundle of the rhizome and of the aerial stem. Both transverse and longitudinal sections were made of the rhizome and the writer was unable to find spiral tracheæ, although they occur in the aerial stem just as they occur in the other grasses. The investigation which followed then resolved itself into a study of the vascular strands: (1) the difference in the vascular structure of the aerial and subterranean stems, (2) the origin, development, and final organization of the vascular bundle of the stems, and (3) the development of the thickenings of the cell walls of the xylem vessels.

When one goes into the literature for a discussion of the above points there is an absence of definite data. Almost all the texts and reference books deal with the mature structures without taking up their origin and development. The figures that are used are mainly those of Zea, and only occasionally is some other grass figured. But though the vascular bundles of the aerial parts of grasses have many similarities, they are not all like corn and they are not all arranged in the stem, as they are in corn. It is possible because of these variations among the grass tribes to identify many genera and even species by their vascular anatomy. Schwendener, Duval-Jouve, Holm, Beal, Pammel, and others have studied the vegetative structures for the purpose of identification; and most of the anatomical studies have been of this type. For these studies in most

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instances the aerial parts were used. But in the grasses the stems vary in the composition of the mature vascular strand and in the arrangement of the vascular bundles, so that not only may the aerial stems of different species be dissimilar, but furthermore, (1) the underground stems of species are different and may form a basis for identification and (2) the aerial and underground stems of the same species are different from each other.

The writer has been unable to find papers which discuss the variation in the vascular anatomy between the rhizome and aerial stem of the same plant, or any discussing the origin and development of the vascular strands of the grasses.

THE RHIZOME.

The internode of the rhizome of *Calamovilfa* is very little elongated. There are few cells of the rhizome which are not lignified. All of the cells of the vascular bundle are thick walled and lignified, even those of the phloem (Fig. 1), although microchemical tests show that the cells of the phloem are not as highly lignified as those of the xylem and pericycle. The reduced leaves, merely scales, are also highly lignified and cutinized. The vascular bundle in the rhizome consists of the phloem with its sieve tubes and companion cells, protoxylem tracheids, and two to four large metaxylem tracheæ. It is without protoxylem annular or spiral tracheæ (Fig. 1), except in an occasional internode which has elongated or in a leaf trace. Instead, the protoxylem cells are thick walled, angular tracheids, and the pericycle is of thick walled, angular cells several layers wide. It forms a continuous band about the stele and the cortex on the inner side. The endodermis is not always well defined.

THE AERIAL STEM.

The aerial stem of *Calamovilfa* shows no differentiation of cortex, for the vascular strands are scattered through the stem around a central pith. Each bundle is surrounded by a thick walled pericycle of several cell layers, and the phloem is made up of large, thin walled sieve tubes with companion cells usually irregularly placed, although they are sometimes quite regular. There are usually two large metaxylem pitted vessels,

and from one to five annular and spiral vessels of the protoxylem surrounded by a few parenchyma cells, (Fig. 2).

The internode is said to develop basipetally. The writer has been unable to demonstrate any definite region of dividing cells at the base of the internode. The elongation in *Calamovilfa* occurs evidently from a diffuse region there which does not continue as cambium activity does, but is of limited development. Lignification begins at the top of the internode and progresses down the stem. The lignification of the base of the internode is the limit of the elongation phase of its development.

THE DEVELOPMENT OF THE INDIVIDUAL VASCULAR BUNDLE.

The desmogen strand is recognized first in the leaf primordium in both longitudinal and transverse sections. It begins with a single cell (Fig. 3), found and recognized with difficulty, that divides into two cells which are readily distinguished, (Fig. 4). Each of these cells divides longitudinally forming four cells (Fig. 5), and from here on the divisions are irregular. The cells of this strand press against the cells surrounding them and cause them to be elongated at right angles to the axis of growth (Fig. 6). This produces an appearance, which later disappears, of a sheath around the demogen strand.

When the strand reaches the condition shown in Figure 7, some of the cell walls both on the inner and outer edge of the strand may begin to thicken, but if elongation is rapid the thickening on the outer edge of the strand does not begin until after the metaxylem cells are differentiated. These outer cells, whose walls become thickened, are pericycle cells.

1. *The Development of the Vascular Bundles of the Aerial System.*

The cells which become thickened on the side of the strand toward the center of the stem are the annular and spiral tracheae of the protoxylem. From one to five of these are differentiated. The mature condition is usually as follows: The first vessel is an annular one with the rings closer together than the first, or a spiral vessel very much stretched out. The succeeding ones formed centrifugally are spirals less and less elongated,

and the youngest either has the tightest spiral or may be a reticulate vessel. Figures showing this are to be found in a number of text and reference works. Metaxylem vessels (pitted vessels when mature) appear after this; the phloem is differentiated about the same time. The metaxylem vessels are formed from the cells at the periphery of the strand (Fig. 8) in the inner half of the bundle, and the phloem begins to develop from the outer portion of the outer half of the bundle and develops centripetally.

At the outer edge of the strand the walls of the pericycle cells begin to thicken and lignification of the bundle begins. This continues until only the phloem cells and a few cells about the annular and spiral vessels remain as thin walled cells.

The protoxylem develops centrifugally, and the phloem develops centripetally for a time; then the cells of the phloem enlarge and in doing so press against the cells between them and the protoxylem so that these cells are flattened to appear as a cambium region. Chrysler has reported cambial activity in the grass bundle, but in *Calamovilfa* although the mature bundle of the aerial parts appears to have a cambium, it certainly does not, for the condition shown in Figure 9 is brought about in the manner described above. The divisions of the cells of the strand, before the xylem and phloem are differentiated, takes place throughout the whole strand as is shown by the accompanying figure (Fig. 10). Consequently the cells may continue to divide between the xylem and phloem in the region just above the nodes (Chrysler) which is the last to be completely lignified, and the pressure of the developing xylem and phloem causes the cells to take on the appearance of a cambium.

2. The Development of the Vascular Bundles Without Annular and Spiral Vessels.

The bundle (Fig. 1) found in the slow growing rhizome develops in a different manner. The desmogen strand develops just as in the bundle described above until the strand is made up of from twenty to fifty cells. Then there appear usually two (at times one to four) large cells which form the large pitted vessels of the bundle (Fig. 11). The cell walls of the pericycle at the outer edge of the bundle begin to thicken and the cells of the protoxylem become lignified, but no annular

or spiral vessels are differentiated (except occasionally one and exceptionally two small ones) and all of the protoxylem cells are tracheids. The lignification, which started with the thickening of the cell walls of the pericycle and protoxylem, now continues until all of the cells of the bundle are thick walled and lignified (Fig. 1).

THE AMPHIVASAL BUNDLE.

The amphivasal bundle (Figs. 12 and 13) which one finds in the nodes and rhizome is brought about by the laying down of two vascular strands together which diverge and continue each as single strands. Sometimes the protoxylem vessels are not laid down, but usually in the aerial stem they are. Figure 12 shows the amphivasal bundle without annular or spiral vessels and Figure 13 shows an amphivasal bundle with a protoxylem spiral vessel. Chrysler has studied this condition in his paper on "The Nodes of Grasses" and states that the amphivasal bundle of the nodes is the fusion of two bundles and that in the basal portion of the plant this may continue through the internode. He also points out that the amphivasal bundle occurs more frequently in the rhizome and lower nodes of the plant than in the aerial nodes. This was found by the writer to be true in *Calamovilfa*. In *Zizania*, Chrysler finds that the amphivasal condition is most common where the nodes are crowded and that the same thing is true in the reproductive branch of corn, where the nodes are also crowded. Since the amphivasal bundle is so closely associated with the amount of elongation and the separation of the vascular strands, it is evident that here may be a means of studying the scattered vascular bundle that will lead to a better understanding of this condition in monocotyledons. That these structures will fit into the ordinary phylogenetic classification is not at all assured, although considered with other characters they may straighten up the relationships of the tribes and genera. Dr. Land, in his lectures, points out the great influence of the pericycle in the breaking up of the stele as the cambium activity becomes less pronounced. There is no doubt that a study of the pericycle and its development as well as a study of the endodermis will be of value for further investigations of the grasses and their inter-relationships.

THE MARKINGS OF THE XYLEM VESSELS.

According to Haberlandt there are five types of mature tracheæ in the xylem: annular, spiral, sclariform, reticulate, and pitted. All of these but the sclariform are found in *Calamovilfa*. As to the cause of the formation of these varying types, Haberlandt, Jeffrey, and others call attention to the fact that the annular and spiral vessels are related to the elongation of the stem or root, but they do not impress upon the reader the fact that annular and spiral thickenings are the direct result of elongation. Some writers even give the idea to their readers that they are annular and spiral to permit elongation rather than that they are the result of elongation.

In the rapidly growing aerial stem the first vessel to be laid down is usually observed to be either annular or spiral, succeeding vessels are closer spirals, and the last formed are reticulate or pitted. The writer finds that the type of vessels found in the mature condition varies with the amount of elongation, while the deposition of material forming the wall thickenings is going on. In very slow-growing stem tips no spirals are found, except occasionally a very tight one and occasionally an annular vessel. In elongating tips annular and spiral vessels of varying degrees are found in the protoxylem. The metaxylem tracheæ, laid down when elongation has practically ceased, are pitted vessels, or may be slightly reticulate.

In the rhizome with very short internodes the annular tracheæ are found occasionally, but few and scattered. These are the only protoxylem vessels found when any are found at all. In fast growing regions of the plant there are as many as five protoxylem annular and spiral vessels in the vascular bundles. In the internodes which are most elongated the elongation may be so great that the annular vessels are actually ruptured and even the surrounding parenchyma cells may be torn so that one finds the thickenings attached along the sides of a cavity. This is figured by Strasburger (page 122), and the cavity is readily demonstrated in corn and other grasses with a rapid development of aerial parts.

The above observation leads to a more careful study of the beginnings of these thickenings. Elongation occurs before these thickenings are lignified, and the thickened portion of the

wall must be, therefore, in a more or less plastic state. A careful examination of the longitudinal sections of the desmogen strands showed that the first thickening is laid down in the pitted form, (Fig. 14). Still younger cells show a vacuolation of the cytoplasm, (Fig. 15), which causes it to line the wall in the same pattern as shown by the first wall thickenings. Apparently then, division and enlargement of the surrounding cells (Fig. 16) tears apart this wall thickening (Fig. 14) and the cell becomes annular, spiral or reticulate, depending upon the amount of stretching. If elongation has ceased, as it has when the thickenings of the metaxylem vessels occur, the wall remains in a pitted condition. In text figures one usually sees these vessels with the spirals and annular rings very regular. This is true to a remarkable degree; but there are many exceptions to this, for irregularity is common.

Thus it is shown that the types of tracheæ vary with the amount of elongation, maximum stretching causing the formation of the annular vessel, decreasing degrees of elongation causing spirals, reticulate, and finally pitted vessels, in the order named. This accounts for the fact that one does not find annular or spiral vessels in secondary wood, where sclariform, reticulate and pitted vessels occur.

It is common knowledge that plant structures vary when under different environmental conditions and it is evident from this study that the vascular structures are possibly not as static as they have been regarded, since the form of the protoxylem tracheæ, as well as the number of tracheæ, varies with the amount of elongation of the internode.

The physiology of the deposition of the thickenings of the xylem vessels is an open question. It may be that subsequent observations of anatomical variations of plants in extreme situations may throw some light upon the reasons for the thickening of the walls laid down in specific cells. It is known that less lignification occurs in hydrophytic than in xerophytic habitats, but this is a secondary thing, for, in *Calamovilfa* at least, lignification occurs after considerable thickening of the cell wall has taken place.

The failure of certain cells to divide in one plane and the ability to divide in another is the thing that leads to the development of the xylem vessels. The reason underlying the failure

of the division at right angles to the main axis of the region of growth can at present be only a conjecture. (Dr. Land).

That the continued division and enlargement of the surrounding cells functions in the elongation of the protoxylem cells was called to our attention by Dr. Land from his work, as yet unpublished, on the origin of conductive strands. As soon as the division of the cells surrounding the xylem vessels ceases there are no more spiral vessels formed and all of the metaxylem vessels remain in the pitted condition.

The writer is indebted to Dr. W. J. G. Land for his advice and constructive criticisms, to Dr. E. N. Transeau for securing the equipment necessary to make these studies, and to the members of the staffs of both the University of Chicago and The Ohio State University for their help given unstintingly whenever it was asked.

SUMMARY.

1. The first appearance of the vascular strands of *Calamovilfa* is the leaf primordia.

2. The vascular strand starts with a single cell.

3. In the elongating parts the order of development is as follows: Annular and spiral protoxylem elements, differentiation of phloem and metaxylem at about the same time, and finally pericycle.

4. In the rhizome the vascular strand does not develop the annular and spiral protoxylem elements because of the failure of the elongation of the internode.

5. The amphivasal bundle of the nodes is brought about by the laying down of two bundles together which later diverge as simple strands.

6. There is no cambial activity in the vascular bundle of *Calamovilfa*.

7. A definite layer of dividing cells has not been found at the base of the internodes, but instead elongation occurs from a diffuse region of dividing cells.

8. The amount of elongation determines whether the tracheæ are annular, spiral, reticulate or pitted vessels.

9. The first thickening of all types of the tracheæ is pitted, and the walls are then stretched out by the division and enlargement of the surrounding cells so that they assume their mature form.

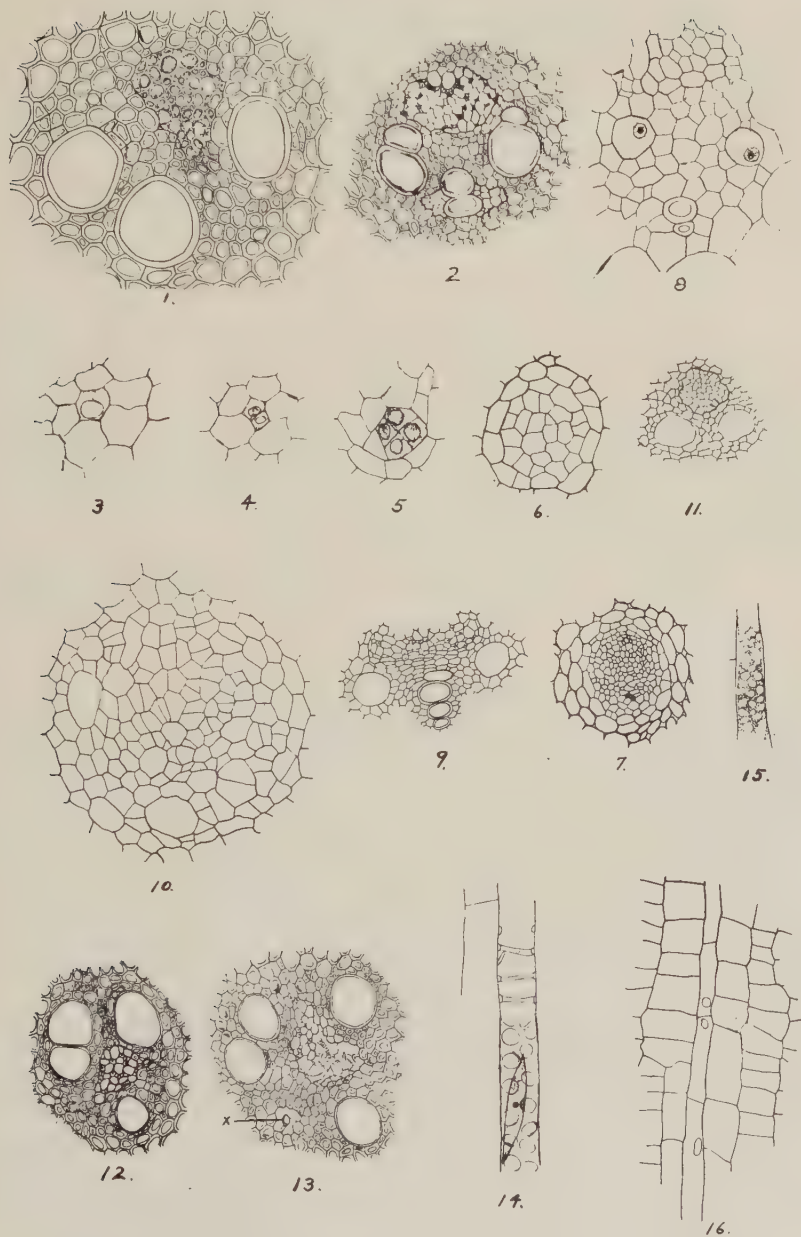
10. The original pitted thickening evidently arises by the vacuolation of the cytoplasm, this thickening being laid down by the thicker portions of the cytoplasm.

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EXPLANATION OF FIGURES.

- Fig. 1. Vascular bundle of rhizome, no protoxylem vessels, phloem lignified.
Fig. 2. Vascular bundle of aerial stem, protoxylem vessels, (P).
Figs. 3, 4 and 5. Development of desmogen strand from single cell to four-celled stage.
Fig. 6. Desmogen strand showing appearance of sheath which disappears.
Fig. 7. Young vascular bundle showing beginning of lignification. The lower thickened cells are protoxylem vessels, the upper the first cell's of the pericycle to be lignified.
Fig. 8. Young vascular bundle of aerial stem showing two protoxylem vessels and the beginning of the differentiation of metaxylem vessels and the phloem.
Fig. 9. Cross section of vascular bundle just above the node of aerial stem, showing four protoxylem vessels (one not showing thickening), and semblance of cambium.
Fig. 10. Desmogen strand showing the irregular division of cells throughout the strand.
Fig. 11. Young bundle of rhizome without protoxylem vessels, but showing the beginning of the differentiation of metaxylem vessels and phloem.
Fig. 12. Amphivasal bundle without protoxylem vessels.
Fig. 13. Amphivasal bundle showing a protoxylem spiral vessel, (X).
Fig. 14. A protoxylem cell showing the original pitted thickenings and spiral thickening in the same cell. The nucleus often remains after the cytoplasm disappears.
Fig. 15. Protoxylem cell showing characteristic vacuolation of the cytoplasm.
Fig. 16. Longitudinal section showing original cell of desmogen strand and divisions of surrounding cells which on enlargement stretch the cells in line with (X).



SOME NEW FORMS OF SPIROGYRA AND OEDOGONIUM*

L. H. TIFFANY

Department of Botany, Ohio State University

In collections of algæ from northwestern Iowa during† the summer of 1923 and from Ohio during the past four years, there have appeared some forms of *Spirogyra* and *Oedogonium* not previously described. In each of the following descriptions a Latin as well as an English diagnosis is given, supplemented by camera lucida drawings. In addition, notes are given on dates and places of collection and on relationships of each form of algæ described. There is appended a short discussion on the importance of knowing the manner of growth of groups of algæ, like the *Oedogoniaceæ*, if the collector desires to make a complete survey of any algal habitat.

The thanks of the writer are due Professor R. B. Wylie for the opportunity of collecting algæ in Iowa, and to Professor E. N. Transeau for critical suggestions given throughout the study of these new forms.

Spirogyra echinata nov. sp.

Cellulis vegetativis $88-96\mu$ latis, diametro 1-2-plo longioribus; dissepimentis planis; chromatophoris 4-7, anfractibus .5-1.5; vellulis fructiferis abbreviatis, et uno latere (in quo conjugatio sequitur) inflatis; zygosporis ovoideis, maturitate bruneis, crass. $68-85\mu$, diam. $76-120\mu$, mesosporio echinato.

Vegetative cells $88-96\mu \times 84-160\mu$, with plane end walls; 4-7 chromatophores making .5 to 1.5 turns; fertile cells shortened and inflated on the conjugating side; zygosporis ovoid, $68-85\mu \times 76-120\mu$, often placed transverse to the filament; median spore wall echinate, brown.

This species has an appearance, in general, similar to that of *Spirogyra rheinhardtii* Chmiel. and of *S. diluta* Wood. From the former it differs in dimensions and number of chromato-

*Papers from the Department of Botany, The Ohio State University, No. 148.

†The writer, upon the invitation of Professor R. B. Wylie, Head of the Department of Botany, The Iowa State University, spent the summer of 1923 at the Iowa Lakeside Laboratory, near Milford, Iowa. Several hundred collections of algæ were made in the vicinity of the Laboratory. A systematic account of all the filamentous algæ found in these collections is in progress.

phores. From both it differs markedly in having the middle wall of the zygospore very prominently echinate, the length of the echinate protuberances ranging from 6 to 9μ . This alga was collected from a cut-off of the Little Sioux River near Montgomery, Iowa, July 17, 1923. Type in Iowa collections herb. L. H. T. Collection No. 121. Plate I, Fig. 1.

Spirogyra pellucida Kuetz. var. *minor* nov. var.

Cellulis vegetativis $30-36\mu$ latis, diametro 2-3-plo longioribus; zygosporis, crass. $40-56\mu$, diam. $50-64\mu$; ceterum ut in typo.

Vegetative cells $30-36\mu \times 73-100\mu$; zygospores $40-56\mu$ in thickness, $50-64\mu$ in diameter; otherwise as in the type.

This variety is easily distinguished from the type by its smaller dimensions throughout, particularly of the zygospores. *Spirogyra pellucida* Kuetz. apparently has not so far been recorded from America. The variety was collected by Mr. B. S. Meyer of the Department of Botany, the Ohio State University, in Baumgardner's Pond near Columbus, Ohio, May 3, 1923. Type in L. H. T. collections No. 354. Plate I, Fig. 2.

Oedogonium iowense nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis vel binis, globosis vel ellipsoideo-globosis, operculo apertis, circumscissione superiore; oosporis eadem forma ac oogoniis, oogonia complentibus vel non complentibus, membrana lævi; antheridiis ad 25-cellularibus; spermatozoidis binis, divisione horizontali ortis; cellula fili, basali forma, ut vulgo, elongata;

crassit. cell. veget.....	$10-16\mu$;	altit. 44-100 μ ;
“ oogen.....	$52-60\mu$;	“ 60-80 μ ;
“ oospor.....	$45-56\mu$;	“ 50-64 μ ;
“ cell. antherid.....	$10-12\mu$;	“ 10-20 μ ;
“ cell. basal.....	$16-24\mu$;	“ 60-80 μ .

Dioecious, macrandrous; oogonia single or in groups of two, globose or ellipsoid-globose, operculate, division superior; oospores of the same form as the oogonia which they completely fill or not, membrane smooth; antheridia 1-25 celled, sperms two, division horizontal; basal cells of filament commonly elongated;

Diam. veg. cells.....	$10-16\mu$;	length 44-100 μ ;
“ oogonia.....	$52-60\mu$;	“ 60-80 μ ;
“ oospores.....	$45-56\mu$;	“ 50-64 μ ;
“ antheridial cells.....	$10-12\mu$;	“ 10-20 μ ;
“ basal cells.....	$16-24\mu$;	“ 60-80 μ .

This species bears some resemblance to *Oe. welwitschii* West, from which it differs in having smaller vegetative cells and larger oogonia. It differs from *Oe. pringsheimii* Cram.; Wittr. in having larger oogonia and oospores. The fact that the fruiting cells have a diameter of 3-6 times that of the vegetative cells gives this form a distinct place among the globose operculate species of *Oedogonium*. It was collected during July and August, 1923, in sloughs and bayous of West Lake Okoboji, Iowa. Type in Iowa collections herb. L. H. T. Collections No. 161, 194, 213. Plate III, Figs. 1-3.

Oedogonium latiusculum nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis vel binis, globosis vel ellipsoideo-globosis, operculo apertis, circumscissione mediana, latissima; oosporis eadem forma ac oogoniis, oogonia complentibus vel fere complentibus, membrana lævi; plantis masculis paullulum crassioribus quam femineis; antheridiis unicellularibus, saepe cum cellulis vegetativis alternis; spermatozoidis singulis; cellulis vegetativis evidenter capitellatis; cellula fili basali subhemisphærica, non elongata; filis haud raro calce incrustatis;

crassit. cell. veg. fem.....	10-18 μ ;	altit. 16-40 μ ;
" cell. veget. masc.....	14-20 μ ;	" 16-40 μ ;
" oogon.....	32-36 μ ;	" 32-40 μ ;
" oospor.....	28-32 μ ;	" 28-34 μ ;
" cell. antherid.....	14-18 μ ;	" 12-20 μ ;
" cell. basal.....	16-24 μ ;	" 12-16 μ .

Oedogonium dioecious, macrandrous; oogonia single or in groups of two, globose to ellipsoid-globose; oogonium operculate, division median, very wide; oospores of the same form as the oogonia, which they very nearly or completely fill, wall smooth; male plants somewhat larger than the female; antheridia unicellular, usually separated by a single vegetative cell, sperm one; vegetative cells distinctly capitellate; basal cell of filament subhemispherical, not elongated; filaments not infrequently incrustated with lime;

diam. veg. cells, female.....	10-18 μ ;	length 16-40 μ ;
" veg. cells, male.....	14-20 μ ;	" 16-40 μ ;
" oogonia.....	32-36 μ ;	" 32-40 μ ;
" oospores.....	28-32 μ ;	" 28-34 μ ;
" antheridial cells.....	14-18 μ ;	" 12-20 μ ;
" basal cells.....	16-24 μ ;	" 12-16 μ .

This species is evidently near *Oe. pratense* Transeau, but differs in its much shorter and distinctly capitellate vegetative cells, in the shape of its basal cells, and in the differently shaped operculate oogonium with its wide opening. The dioecious habit

and the distinctly capitellate vegetative cells easily separate it from *Oe. acmandrium* Elfv. and from *Oe. psægmatorum* Nordst. From *Oe. capitellatum* Wittr. it is further distinguished by its larger dimensions throughout. It was collected in June, July, and August, 1923, in Miller's Bay of West Lake Okoboji, in the East Bay of Spirit Lake, in Clear Lake, and in Swan Lake, Iowa. Type in Iowa collections herb. L. H. T. Collections No. 7, 146, 168, 212. Plate III, Figs. 4-6.

Oedogonium infimum nov. sp.

Oedogonium dioicum, macrandrium; oogoniis singulis, globosis vel subglobosis (vel interdum parte basali paullo magis evoluta subpyriformi-globosis), operculo apertis, circumscissione infima; oosporis globosis vel subdepresso-globosis, oogonia fere complentibus, membrana lævi; plantis masculis paullo crassioribus quam femineis; antheridiis 1-10 cellularibus, spermatozoidis binis; cellulis vegetativis evidenter capitellatis; cellula fili basali subhemisphærica, non elongata; filis haud raro calce incrustatis;

crassit. cell. veget. fem.....	12-18 μ ;	altit. 60-140 μ ;
" cell. veget. masc.....	16-20 μ ;	" 60-140 μ ;
" oogon.....	40-48 μ ;	" 41-50 μ ;
" oospor.....	40-44 μ ;	" 38-42 μ ;
" cell. antherid.....	14-20 μ ;	" 8-12 μ ;
" cell. basal.....	30-42 μ ;	" 16-24 μ .

Oedogonium dioecious, macrandrous; oogonia single, globose or subglobose (or the basal part extended, appearing subpyriform-globose); operculate, division at the lowest extremity of the oogonium; oospores globose or subglobose, membrane smooth; male plants a little larger than the female; antheridia 1-10 celled, sperms two; vegetative cells distinctly capitellate; basal cell of filament subhemispherical, not elongated; filaments not infrequently incrustated with lime.

diam. veg. cells, female.....	12-18 μ ;	length 60-140 μ ;
" veg. cells, male.....	16-20 μ ;	" 60-140 μ ;
" oogonia.....	40-48 μ ;	" 41-50 μ ;
" oospores.....	40-44 μ ;	" 38-42 μ ;
" antheridial cells.....	14-20 μ ;	" 8-12 μ ;
" basal cells.....	30-42 μ ;	" 16-24 μ .

This species bears some resemblance to *Oe. inversum* Wittr. and the variety *subclusum* (Wittr.) Hirn. It differs from both in its larger dimensions and in having the male filaments larger than the female. The decidedly basal division of the operculate oogonium is its chief distinctive character. Hirn* in his

*Hirn, Karl E. Monographie und Iconographie der Oedogoniaceen. Helsingfors. 1900, p. 43.

tabular arrangement of the species of *Oedogonium* makes seven subdivisions of the globose, operculate forms, depending upon the position of the division of the oogonium. These subdivisions are: "Circumscissio: suprema, superior, supramediana, mediana, inframediana, inferior, infima." Hirn records no form of *Oedogonium* belonging to the group "Circumscissione infima." This, therefore, is apparently the first record of any species, either poriferous or operculate, belonging in that class; to designate such a decidedly basal opening the specific name *infimum* (*L. infimus*, lowest) is given. The outer spore wall, when not fully mature, sometimes appears slightly undulate, but this must not be taken to indicate an *Oedogonium* with rough-walled spores. So far this species has been recorded from Swan Lake and Clear Lake, Iowa, collected during July and August, 1923. Type in Iowa collections herb. L. H. T. Collections No. 146, 155, 231. Plate II, Figs. 6-9.

Oedogonium exospirale nov. sp.

Oedogonium dioicum, nannandrium, idioandrosporum; oogoniis singulis vel rarius binis, subglobosis vel oboviformi-globosis (rarius subhexagonis), poro mediano apertis; oosporis globosis vel subglobosis, oogonia fere complentibus, membrana duplici: episporio costis spiralter dispositis, costis spiralibus numero 5-8, utrinque in polo, in sectione horizontali, fere mediano, nunquam verticali sito conniventibus, endosporio lævi; cellulis suffultoribus tumidis; androsporangiiis 1-6 cellularibus; cellula fili basali forma, ut velgo, elongata; nannandribus paululum curvatis, in cellulis suffultoribus sedentibus, antheridio exteriore, 1-3 cellulari;

crassit. cell. veget.....	8-12 μ ;	altit. 60-88 μ ;
" cell. suffult.....	16-28 μ ;	" 60-88 μ ;
" oogon.....	40-44 μ ;	" 44-48 μ ;
" oospor.....	32-38 μ ;	" 38-40 μ ;
" cell. andros.....	12-16 μ ;	" 14-20 μ ;
" stip. nannandr.....	14-16 μ ;	" 30-40 μ ;
" cell. antherid.....	8-12 μ ;	" 14-16 μ .

Oedogonium dioecious, nannandrous, idioandrosporous; oogonia single or rarely in groups of two, subglobose or oboviform-globose (rarely subhexagonal), pore median; oospores globose or subglobose, nearly filling the oogonia, membrane double, outer spore wall marked by 5-8 spiral ribs uniting at the poles, the polar axis always placed in a transverse position, never parallel with the filament, the inner spore wall smooth; suffultory cells swollen; androsporangia 1-6 celled; basal cells elongate; dwarf males a little curved, situated on the suffultory cells, with exterior antheridia 1-3 celled;

diam. veg. cells.....	8-12 μ ;	length	60-88 μ ;
" suffultory cells.....	16-28 μ ;	"	60-88 μ ;
" oogonia.....	40-44 μ ;	"	44-48 μ ;
" oospores.....	32-38 μ ;	"	38-40 μ ;
" androsporan. cells.....	12-16 μ ;	"	14-20 μ ;
" dwarf male stipe.....	14-16 μ ;	"	30-40 μ ;
" antheridial cells.....	8-12 μ ;	"	14-16 μ .

Forms of *Oedogonium* nearest this species are *Oe. illinoiense* Transeau and *Oe. spirale* Hirn. From both it differs in the considerably smaller dimensions of the vegetative and fruiting cells. It further differs from the former in being idioandrosporous. It is readily separated from *Oe. huntii* Wood by the median position of the pore of the oogonium and by its dimensions. The form was recorded from the East Bay of Spirit Lake and from a slough north of West Lake Okoboji, Iowa, during July and August, 1923. Type in Iowa collections herb. L. H. T. Collections No. 161, 168. Plate II, Figs. 1-3.

Oedogonium supremum nov. sp.

Oedogonium dioicum, nannandrium, idioandrosporum; oogoniis singulis vel rarius 2-4 continuis, globosis vel ellipsoideo-globosis, sæpe terminalis; operculo apertis, circumscissione surpema, operculo sæpe deciduo; oosporis eadem forma ac oogoniis, hæc plaen complementibus, membrana lævi; cellulis suffultoriis eadem forma ac cellulis ceteris; androsporangii 1-6 cellularibus; cellulis vegetativis evidenter capitellatis; cellula fili basali forma, ut vulgo, elongata; nannandribus late oboviformibus, unicellularibus, in oogonis sedentibus;

crassit. cell. veget.....	24-32 μ ;	altit.	60-132 μ ;
" oogon.....	66-78 μ ;	"	72-90 μ ;
" oospor.....	60-66 μ ;	"	66-84 μ ;
" cell. andros.....	26-28 μ ;	"	30-40 μ ;
" nannandr.....	20-24 μ ;	"	24-26 μ ;
" cell. basal.....	28-32 μ ;	"	90-110 μ .

Oedogonium dioecious, nannandrous, idioandrosporous; oogonia single or rarely in groups of 2-4, globose or ellipsoid-globose, often terminal, operculate, division at the upper extremity of the oogonium, lid often deciduous; oospores of the same form as the oogonia which they completely fill, membrane smooth; suffultory cells of the same form as the other vegetative cells; androsporangia 1-6 celled; vegetative cells distinctly capitellate; basal cell of the filament elongated; nannandrium broadly oboviform, unicellular, situated on the oogonia;

diam. veg. cells.....	24-32 μ ;	length	60-132 μ ;
" oogonia.....	66-78 μ ;	"	72-90 μ ;
" oospores.....	60-66 μ ;	"	66-84 μ ;
" androsporan. cells.....	26-28 μ ;	"	30-40 μ ;
" dwarf males.....	20-24 μ ;	"	24-26 μ ;
" basal cells.....	28-32 μ ;	"	90-110 μ .

This species is nearest *Oe. praticolum* Transeau and *Oe. obtruncatum* Wittr., from both of which it differs in having much larger dimensions and differently shaped oogonia and oospores. The terminal cells are not apiculate. It differs from *Oe. kitutae* West in being operculate, and in the general form of the vegetative and fruiting cells. Since this species is one of the few forms whose operculate division is at the upper extremity of the oogonium, the specific name *supremum* (L. *supremus*; highest) is applied. It was found in West Lake Okoboji, Iowa, during August, 1923. Type in Iowa collections herb. L. H. T. Collection No. 194. Plate I, Figs. 3 and 4; Plate II, Figs. 4 and 5.

Oedogonium grande Kuetz.; Wittr. var. *robustum* (Hirn) nov. comb.
Hirn: Monographie und Iconographie der Oedogoniaceen, p. 144, 1900.

Var. *omnibus partibus crassioribus*;

crassit. cell. veget. fem.	32-46 μ ;	altit.	80-200 μ ;
" cell. veget. masc.	32-42 μ ;	"	80-200 μ ;
" oogon.	52-68 μ ;	"	75-90 μ ;
" oospor.	50-64 μ ;	"	68-88 μ ;
" cell. antherid.	30-36 μ ;	"	10-16 μ .

Somewhat larger than the type in all dimensions;

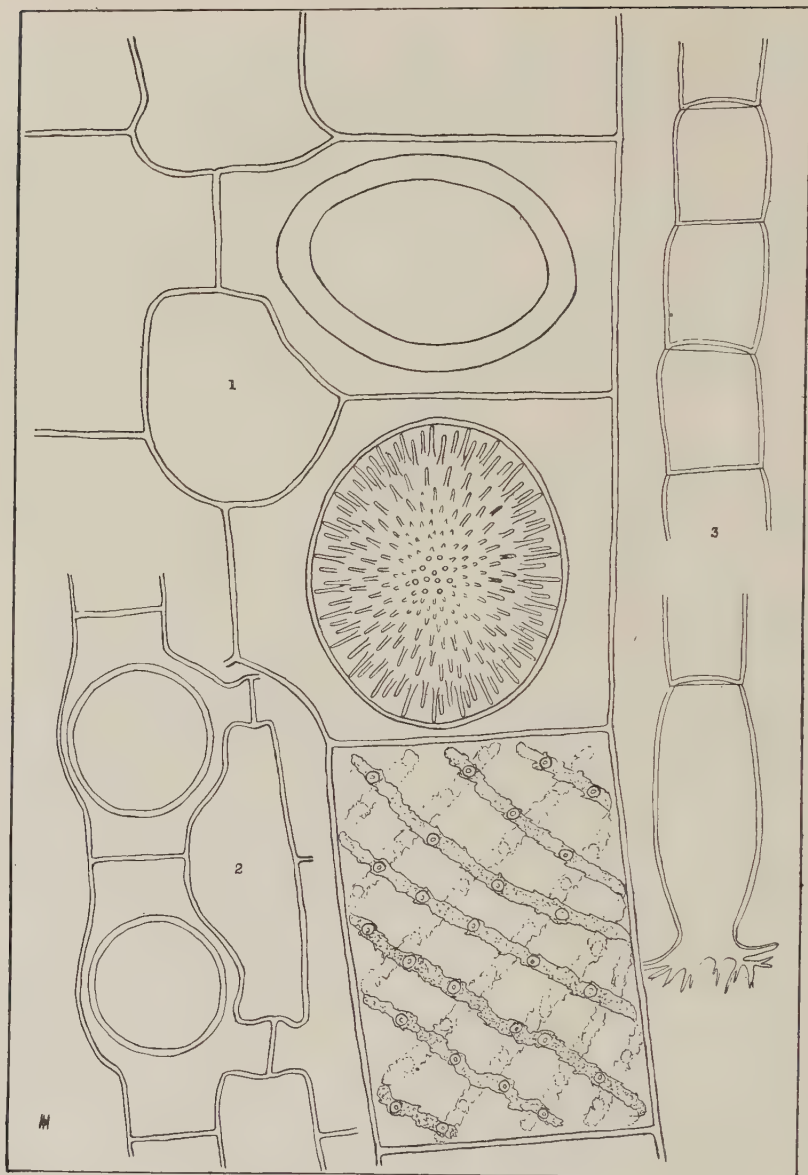
diam. veg. cells, female.	32-46 μ ;	length	80-200 μ ;
" veg. cells, male.	32-42 μ ;	"	80-200 μ ;
" oogonia.	52-68 μ ;	"	75-90 μ ;
" oospores.	50-64 μ ;	"	68-88 μ ;
" antheridial cells.	30-36 μ ;	"	10-16 μ .

Although listed by Hirn as a robust form of *Oe. grande*, its very common occurrence in American material generally, either with the type or separate, seems to warrant a varietal rank. The American forms are considerably larger than the type. This variety along with the type is normally a summer annual, occasionally fruiting as early as June or as late as September. Plate III, Fig. 7.

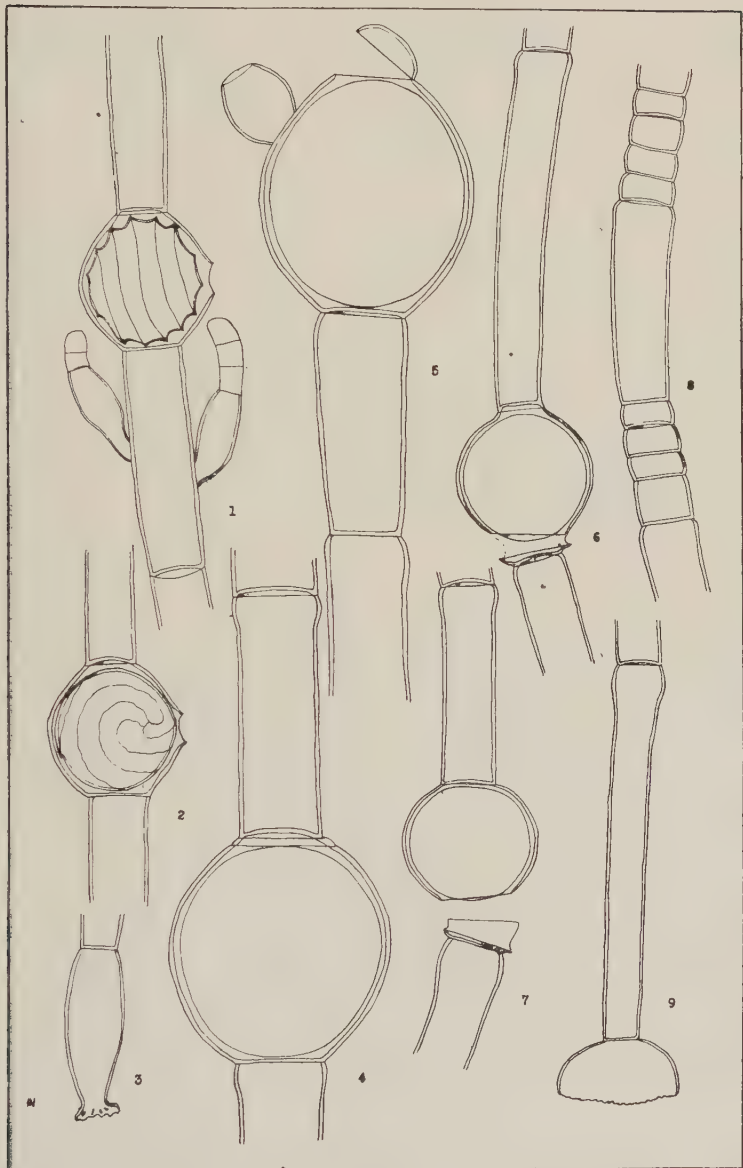
Filaments of *Spirogyra* are usually found free-floating in quiet bodies of water, or remain stationary because they are associated, accidentally or otherwise, with other algæ or flowering plants that are attached to the substratum. It generally is true that one is likely to find a considerable mass of a species of *Spirogyra*, if collections are made in the proper season, instead of isolated individuals.

Species of Oedogonium, on the contrary, may be attached by holdfast cells during their entire vegetative and reproductive periods of growth. Some forms, such as *Oe. capilliforme* Kuetz.; Wittr., *Oe. crassiusculum idioandrosporum* Nordst. et Wittr., *Oe. grande* Kuetz.; Wittr., and *Oe. anomalum* Hirn, frequently form individual or collective masses of considerable size with holdfast cells difficult to find. Such species as *Oe. iowense*, *Oe. latiusculum*, *Oe. infimum*, *Oe. supremum*, and *Oe. exospirale* (described above), as well as many others, including *Oe. inversum* Wittr., *Oe. nanum* Wittr., and *Oe. praticolum* Transeau, are not known to form such masses. They occur as epiphytes on the leaves and stems of submerged higher plants and on species of *Cladophora*, *Pithophora*, and larger Oedogoniums. The number of such epiphytes upon their hosts is usually small and is further reduced pretty close to a minimum in the small sample that makes up the microscopic mount of the material. It is for the reason of this more or less solitary existence that species of Oedogonium are so often overlooked by collectors of algæ, not only in the field but also after they may be safely preserved in collections!

Many of the smaller species of Oedogonium are often so incrustated with such a heavy deposit of lime (mostly CaCO_3) that even generic identification is difficult. If filaments so incrustated are placed on a slide, a few drops of lactic acid added, and the whole gently heated, the entire incrustation is removed without injury to the cells or changes in their dimensions. In addition, the basal cells, often a species criterion, are made perfectly visible.



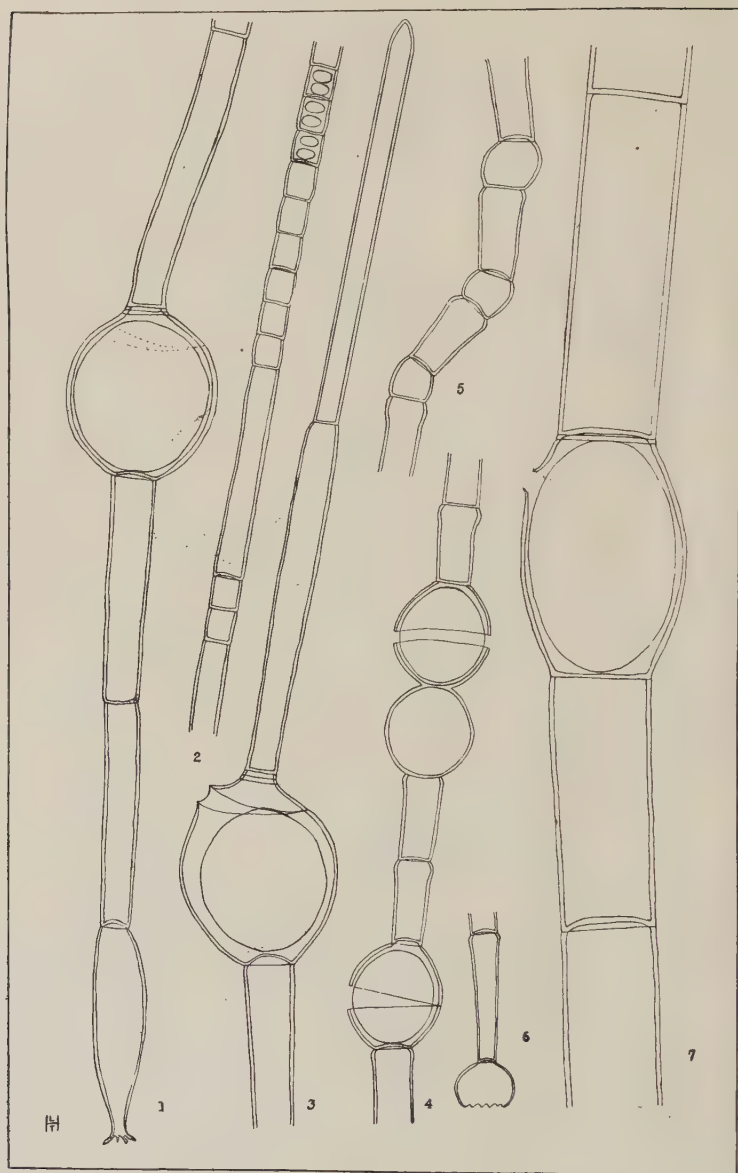
- Fig. 1. *Spirogyra echinata*, showing chromatophores of one vegetative cell, a mature zygospore with echinate protuberances, and the variable position of the spore.
 Fig. 2. *Spirogyra pellucida* var. *minor*.
 Fig. 3. Androsporangial cells of *Oedogonium supremum*.
 Fig. 4. Basal cell of filament of *Oedogonium supremum*.



Figs. 1-3. *Oedogonium exspirale*.

Figs. 4-5. *Oedogonium supremum*.

Figs. 6-9. *Oedogonium infimum*.



Figs. 1-3. *Oedogonium iowense*.

Figs. 4-6. *Oedogonium latiusculum*.

Fig. 7. *Oedogonium grande* var. *robustum*.

NEW PARASITIC HYMENOPTERA OF THE
SUBFAMILY ANTEONINÆ (BETHYLIDÆ).

F. A. FENTON

Department of Zoology and Entomology, Iowa State College.

During 1923, a number of dryinid wasps were bred from several species of *Cicadellidæ* and *Fulgoridæ* collected in Iowa. Upon examination, at least three species were found to be new and are described for the first time in this paper. One of these, namely, *Aphelopus bicolor*, had caused about ten per cent parasitism of its host, *Erythroneura trifasciata* Say. The larvæ of this species have also been collected in Ohio but were not reared through to the adult stage. *Aphelopus comesi* Fent. was also bred from *Erythroneura vulnerata* Fitch, collected at Spring Hill, Iowa. About half of the last named host species which were collected were parasitized.

Pseud ogonatopus iowensis n. sp.

The most striking characteristic of this species is the pale yellow tenth antennal joint, which contrasts sharply with the other dusky joints of the flagellum. Length, 2.81 mm. General color fusco-piceous. Eyes and vertex of head fuscous; frons and occiput, mandibles except teeth, clypeus and scape of antenna testaceous; tenth joint of antenna pale yellow; prothorax ferruginous with black on each side of the transverse emargination; thoracic constriction black, except ventral part and a narrow area down the center of the dorsum, which are testaceous; legs yellow to testaceous, except anterior femora, which are fuscous dorsally; propodeum piceous; abdomen fusco-piceous.

Head.—Vertex slightly concave, broader than long (19:12), surface closely and minutely punctate. Scape of antenna slightly more than twice as long and somewhat thicker than second joint; third about the same thickness as second and more than twice as long; fourth slightly more than half as long as third and somewhat thicker; fifth to eighth inclusive of nearly the same length and width, each being one-fourth shorter and slightly thicker than the fourth and slightly increasing in width towards the tip; ninth shorter than these; tenth less than twice length of ninth and of same thickness.

Thorax.—Prothorax shining with very fine microscopic punctation. Thoracic constriction slightly longer than wide (5:4), with surface minutely roughened, due to fine reticulation.

Propodeum.—Surface with dense punctation; anterior portion with irregular, coarse rugulosity; posterior third beginning just back of the

disc with a series of transverse rugose lines which extend down the sides. Type shows scattered fine white hairs present on this part.

Chela.—(Fig. 3). Median arm with a cluster of lamellæ at the tip and a row extending from a point near this nearly down to the articulation with the lateral arm, the lamellæ being somewhat farther separated from each other near this point. Lateral arm with six smaller, rather widely spaced lamellæ.

Described from one specimen bred from *Liburnia lutulenta* Van Duzee*, Ames, Iowa, July 21, 1923. Type in writer's collection.

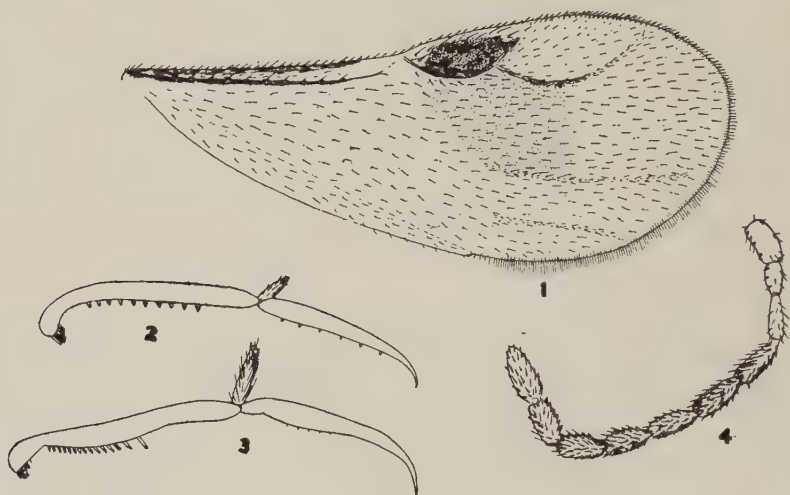


Fig. 1. Fore wing of *Aphelopus bicolor*.
 Fig. 2. Chela of *Pseudogonatopus iowensis*.
 Fig. 3. Chela of *Chalcogonatopus nigrus*.
 Fig. 4. Antenna of *Aphelopus bicolor*.

Aphelopus bicolor n. sp.

A reddish brown species quite distinct from any others with which I am familiar. Length, 1.5–1.59 mm., alar expanse, 1.1–1.2 mm. Head testaceous except compound eyes, which are black, and teeth of mandibles, which are deep amber; first two antennal segments and basal part of third testaceous; rest of antennal segments brown. Mesonotum and scutellum testaceous; post-scutellum and basal portion of propodeum except extreme posterior margin, shining black; rest of propodeum testaceous; legs testaceous, except hind tibiæ and fifth tarsal joints, which are fuscous; fore wings with fuscous band extending below pterostigma and greater part of radius (Fig. 1); abdomen shining

* The host species from which these parasites were bred were kindly determined for the writer by Professor Herbert Osborn.

brown. Head and thorax with fine short pubescence; propodeum with very sparse, indistinct pubescence.

Head.—Broader than deep, (14:8); pattern a fine reticulation. Anterior ocellus slightly closer to the two lateral ones than these are from the hind margin of the head; compound eyes with sparse short, white pubescence. Clypeus arcuate; mandibles four-dentate, with three large teeth and one smaller inconspicuous one; maxillary palpi long and extending considerably beyond base of the head to the thorax, with four joints visible.

Antennæ of median length. First antennal joint slightly thicker and one-fourth longer than second; third of same length as first, somewhat more slender than second; fourth to sixth each one-fifth longer than third and of same thickness as second; seventh to ninth subequal, each being slightly shorter than sixth; tenth three-fifths longer than ninth; from the sixth to the ninth, each succeeding joint is slightly shorter and thicker than the preceding. (Fig. 4).

Thorax.—Mesonotum with same pattern as head; parapsidal furrows distinct, converging and extending about half way to caudal border of mesonotum; scutellum of same pattern as head and mesonotum; postscutellum and propodeum coarsely reticulately sculptured, the reticulations being large, with distinct raised lines. A distinct median smooth area is present on the dorsal posterior part of the propodeum.

Wings.—Fore wings in ratio of 30:13, hind wings, 22:6.

Abdomen.—Compressed laterally, sparsely pubescent.

Paratype. In this specimen the propodeum is entirely piceous on the dorsum, otherwise the coloration is the same.

Bred from *Erythroneura trifasciata* Say, Collected at Spring Hill, Iowa, October, 1922. Type in writer's collection.

Chalcogonatopus nigrus n. sp.

Length 2.448 mm. Black except antennæ, legs, face and a small area on the first abdominal segment, which are fuscous or testaceous. Antennæ fuscous except the first joint, which is testaceous; mandibles testaceous except the teeth; face testaceous just above the bases of the antennæ; compound eyes fuscous. Fore coxæ testaceous, except a fuscous area on the dorsal side extending two-thirds the distance of this joint from its base; fore trochanters testaceous; fore femora fuscous except distal parts at the union with the tibiæ, which are testaceous, somewhat darker dorsally; fore tibiæ fuscous except proximal part near the union with the femora, which are testaceous; fore metatarsi fuscous, rest of fore tarsi, including chelæ, testaceous; incrassate parts of the median and hind legs fuscous. The small tapering part of the propodeum near the petiole is testaceous, as well as a small area on dorsal part of the first abdominal segment just beyond the petiole.

Head.—Broader than long (18:10); slightly concave, showing under high power a very indistinct reticulation which is more distinct

posteriorly from the occipital region to just back of the median ocellus; two spur-like areas of this more distinct reticulation extend forward as far as the median ocellus, but a little to each side of it. Mandibles four-dentate; antennæ long; first joint twice the thickness of the rest, one-third longer than the second; third twice the length of the first, slightly more slender than the second; fourth slightly longer than the first or fifth, which are of the same length, and of the same thickness as the third; sixth, seventh, and eighth of equal length, each being one-fourth shorter than the fifth; ninth short, two-thirds the length of eighth; tenth twice the length of the ninth, same length as first.

Thorax.—The pronotum divided by an arcuate deeply impressed transverse line, the shorter, wider anterior portion being smooth and shining, the narrow elongated posterior division being finely reticulately sculptured. Thoracic constriction longer than wide (7:4) with several distinct longitudinal wrinkles or folds dorsally, extending throughout its length, except anteriorly, where the surface is smooth and polished.

Propodeum.—Propodeum with a distinct transverse rugulosity which also extends down the sides; disc with a fine reticulation. An indistinct, short, scattered pubescence is present.

Chela.—(Fig. 2). Median arm with a cluster of lamellæ at the tip, and a row of smaller ones extending from a point near the tip, half-way down to the articulation of this joint with the lateral arm, the last two lamellæ being longer than the rest.

Described from one specimen bred from *Scaphoideus* sp. probably *immistus* Say, July 8, 1923, collected by C. J. Drake. Type in writer's collection.

SOME OBSERVATIONS ON THE LIFE CYCLE AND
HABITS OF DORYDIELLA FLORIDANA BAKER
(HOMOPTERA-CICADELLIDÆ).

DWIGHT M. DE LONG

Department of Zoology and Entomology, Ohio State University.

While working with *Cicadellidæ* during the past few years, several interesting species have been found and studied. *Dorydiella floridana* is one which has been especially interesting to the writer because of its accidental discovery and in view of the fact that practically nothing was known concerning its habits. It was described by Baker in 1897 from material collected in Florida. During the past twenty-five years it has been taken occasionally in New Jersey, Tennessee, Massachusetts, Pennsylvania, Indiana, Illinois and South Dakota. Its range is therefore quite extensive, although it has been considered as a so-called rare insect and there are very few specimens even in specialists collections. During the summer of 1919 an ecologic study of the leafhoppers of Presque Isle, Pa., was undertaken and this species was collected in general sweeping near one of the numerous lagoons. When it was known that the insect occurred in this area, a detailed search was made to determine under what conditions and upon what plant the insect lived.

It was found to be living on *Scleria verticellata* in the *Eleocharis obtusa* association. Further observations showed that it may be found any place where it is sufficiently moist for the growth of this plant, but the optimum condition apparently for the insect, judging from relative numbers, is on the moist sandy soil within the lagoon basin, but far removed from the receding water. Undoubtedly the reason it has been collected so rarely is due to the fact that it feeds in both nymphal and adult stages on the succulent growth just above the surface of the ground and within the clump. Although only an occasional adult could be obtained by sweeping, several hundred specimens, both nymphs and adults, were obtained by picking apart clumps of *Scleria*. The nymphs were especially difficult to find at first because they were so well concealed between the leaves and so protectively colored. The brownish mottled

color, together with their elongate flattened shape, causes them to resemble so closely the dried blades of grass that their movements alone are responsible for their recognition. The movements of the nymphs especially, and to some extent those of the adults, are very sluggish and even when disturbed they will usually cling to some portion of the plant.

LIFE CYCLE NOTES.

Observations on the life cycle show that there is but one generation a year. The insect overwinters as an egg. These begin hatching in late May or early June, the first adults appearing about the middle of July. Although specimens in nymphal instars are found until September, all of these are late individuals of the first generation. Observations have been made only on the number of instars and the total length of time spent in the nymphal stage. No attempt has been made to obtain data on the length of time for the individual instars. The total length of time from egg to adult is about six weeks. There are five nymphal instars, three of which have been photographed and described here.

DESCRIPTION OF INSTARS.

Second Instar. (Figure 1).

Vertex long and flattened, apex blunt, spoon-like, slightly concave. Vertex longer than thorax, four times longer than pronotum, more than two-thirds as long as entire abdomen. Face with a very prominent keel extending from tip of vertex to clypeus. Sides of face deeply concave from edge of keel to edge of vertex. Length, 4 mm.

Color: Dirty white, irrorate with brown. Tip of vertex with a brownish cross, a rather broad median longitudinal stripe, and a short one next either eye, pale. Eyes red. Three longitudinal pale stripes, a continuation of those on vertex, extending across thorax and abdomen. Each abdominal segment excepting last with a conspicuous black spot either side just above rounded pleural portions. Face dark brown. Edge of keel, margin just below vertex and two oblique lines crossing face, pale. Legs irrorate with brown, venter pale yellow to reddish, a double median longitudinal line and side portions of plates brownish.

Posterior segment of abdomen cleft, forming two pointed projections.

Fourth Instar. (Figure 2).

Length 7 mm.

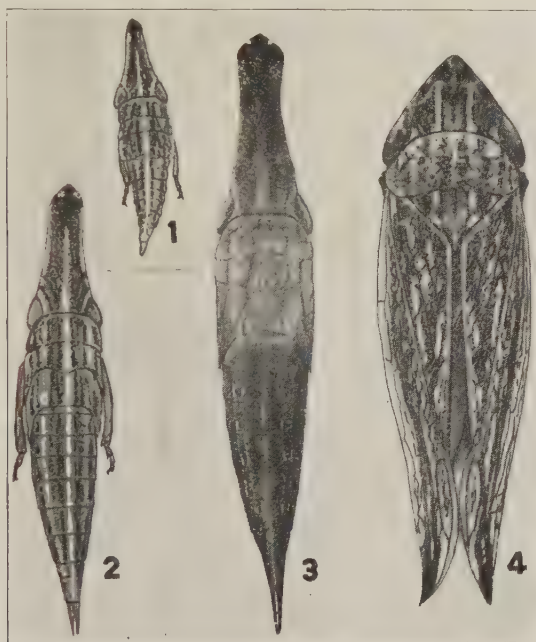
Similar to preceding with abdomen much longer proportionately, almost twice as long as vertex. Vertex about one-fourth longer than thorax. Wing pads only slightly visible. The coloration is very similar to the preceding, except that the markings are more pronounced

in this instar. The dark cross on the tip of the vertex is much more conspicuous. Thorax and abdomen with four rather definite brownish longitudinal lines, separating the three pale stripes. Face dark brown to black with similar pale markings, as in preceding instars.

Fifth Instar. (Figure 3).

Length, 9 mm.

In this, the last nymphal instar, the vertex is longer proportionately. It is considerably longer than the thorax and more than one-half as long as the abdomen. The vertex is even more spoon-shaped than in preceding instars and the apical portion is quite concave. The keel on the face is proportionately larger. Coloration darker and more conspicuous than in preceding instars.



Photographs of the various stages of the life cycle.

Fig. 1. Second instar nymph.
Fig. 2. Fourth instar nymph.

Fig. 3. Fifth instar nymph.
Fig. 4. Adult.

Adult. (Figure 4).

Length, 7 mm.

On comparing the adult and last nymphal instar, it will be noticed that the adult is much shorter, which is rather unusual among the *Cicadellidæ*. Furthermore the vertex is greatly shortened and broadened in the adult. It is only slightly longer than the pronotum and is much shorter than the thorax. The conspicuous keel on the face is lost entirely, and one not familiar with the nymphal stages would scarcely place

nymphs and adults of this insect together as the same species. The elytra are well developed and pointed at the apex. The entire insect is marked with brown irrorations or ramose pigment lines.

PHYLOGENETIC RELATIONSHIP.

In regard to relationship, it is our belief that the earlier stages of any animal give more evidence pertaining to its relationship to other species and its ancestry than we are able to judge from the adult condition. The fact that the nymphal forms exhibit a long foliaceous vertex would certainly place this species with the *Dorydiaria*, which is composed of a group of species with this vertex character. Prof. Osborn* placed it in this position without having seen the nymphal stage and the author† after examining the nymph also allied it with the *Dorydiaria*. Van Duzee‡ has placed it intermediate between *Phlepsius* and *Acinopterus*. The resemblance to *Phlepsius* is more or less superficial, but he has evidently placed it here because in coloration it is brownish irrorate and has definite ramose pigment lines especially on the elytra. In this respect it does resemble a species of that genus. It is true, however, that after the vertex is greatly reduced in the adult stage, the head resembles very closely the foliaceous type of *Phlepsius* head. In the nymphal stages of these *Phlepsius* species, however, so far as the author has been able to examine them, there is nothing to compare with the vertex of the *Dorydiella*. It has been placed close to *Acinopterus* no doubt because of the pointed apex of the elytron. The usual condition is a well rounded apex. In the American *Cicadellidæ* this pointed elytron is found in very few genera. In addition to the *Dorydiella* and *Acinopterus* it is also found in *Dorydium*, which is one of the *Dorydiaria*. Furthermore, the nymphs of *Acinopterus* and *Dorydiella* are entirely different, suggesting diverse affinities, and the adults have very little in common except the pointed elytron, so this would seem to indicate parallel development instead of a close relationship and the emphasis should be placed upon the nymphal characters. In view of the fact we have found only one species belonging to this genus we are able to designate relationship only by the characters of the various stages of this species.

* Ohio Journal Sci., Vol. XX, No. 5, p. 160, 1920.

† Bull. 34, St. Geol. & Nat. Hist. Survey, Conn., p. 91, 1923.

‡ Univ. of Calif. Pub., Tech. Bull. Vol. II, 1917, p. 675.

VARIATIONS IN THE ROOT SYSTEM OF THE COMMON EVERLASTING (*GNAPHALIUM POLYCEPHALUM*).

HELEN GUHMAN

University of Cincinnati

It has been observed that the root system of the common everlasting (*Gnaphalium polycephalum*) has a different behavior when it is grown in different habitats. On well-drained, sloping areas the roots show positive geotropism, that is they grow down, while on poorly drained flat areas the roots show plagiotropism or diageotropism, that is they turn at right angles.

The sloping areas from which the roots were collected were well-drained and consequently well aerated; the flats were either clearings or meadows of the uplands and consequently undrained. In these flats the water table was not far from the surface in late fall, winter, and spring (1). The soil was largely Cincinnati silt loam and Clermont silt loam. The Cincinnati silt loam consists of eight to twelve inches of grayish yellow or light yellowish brown silt loam, having a characteristic mealy or velvety feel. This soil plows up readily and is formed by the weathering of loess on rolling uplands along with the aeration of the soil. Clermont silt loam consists of a layer of seven to twelve inches of light gray or nearly white silt loam. When typically developed it is very ashy, and on the flattest, most poorly drained areas iron concretions are frequently scattered over the surface. The subsoil is of an impervious and compact nature. It possesses practically no power of granulation. Clermont silt loam always develops by the weathering of loess on flat uplands, where there is a deficiency of oxygen. The difference between this soil and the Cincinnati silt loam is due entirely to the difference in drainage. Owing to the level character of the surface on which Clermont silt loam is produced and the impervious nature of the subsoil, natural drainage is very deficient. Hence, there is often found water standing on the surface and this prevents aeration. As a result, humic acid is produced and there is the precipitation of lime, iron, and phosphorus of the soil. Since the soil is limestone, this results in acid on limestone soil (4). The flatness together with the fine impervious soil make the flats very wet. Along with

the excess of water in the soil there is a deficiency of oxygen. Therefore, it is probable that the poor drainage together with the deficiency of oxygen caused the everlasting roots growing on flats to turn. It has been reported (5) that roots show aerotropism, that is, when oxygen diffuses against young roots from one side, the root curves toward the source of the gas.

The everlasting is a winter annual. The seeds germinate very soon after ripening in late fall. The rosettes remain through the winter and spring. In the summer the tall stalks and the flowers of the plants develop. The development of the root system precedes this; therefore the tap root must have developed when the water table was near the surface. The high water table at this time probably accounts for the turning of the roots. The factors which determine the turning of the roots may be an excess of water, deficiency of oxygen, or both. A secondary factor resulting from these two may be soil acidity.

SOIL REACTIONS.

Two hundred and twenty-two roots from various areas—steep slopes, gentle slopes, even flats, and irregular flats, or flats made irregular because they had been plowed at some time—were collected in the late fall after growth had been completed. These roots were observed and placed in one of three classes: I, roots showing positive geotropism; II, roots showing diageotropism; III, roots showing less pronounced diageotropism.

In order to determine whether soil reaction is a factor in deciding direction of root growth, at the time the roots were collected, soil samples were taken from above and below the point of turning if the root turned, or at the top and bottom of the root system if the root did not turn. Later the specific acidity or alkalinity of the soils were determined according to the Wherry field method (6). The results of the observations are given below:

I. ROOTS SHOWING POSITIVE GEOTROPISM. (Fig. 1).

Number	Nature of Area	Reaction at Top	Reaction at Bottom
21	gentle slope	neutral	neutral
15	gentle slope	neutral	sp. acid. 30+
9	gentle slope	sp. alk. 3+	neutral
3	gentle slope	sp. acid. 3+	sp. acid. 3+
16	steep slope	neutral	neutral
16	steep slope	sp. acid. 30+	sp. acid. 30+
1	even flat	sp. acid. 10+	sp. acid. 10+

Of the eighty-one roots showing positive geotropism, eighty of these grew on slopes and one on an even flat. Of these eighty, thirty-two grew on steep slopes (two areas) and forty-eight on more gentle slopes (seven areas). The slopes were well-drained and consequently well aerated.

At the top of the root systems the conditions varied from specific alkalinity 3+ to specific acidity 30+. At the bottom the conditions varied from neutral to specific acidity 30+. From these data it can be seen that there was no relation between the soil reaction and the fact that the roots grew down. Positive geotropism is not due to the specific alkalinity or acidity of the soil.

II. ROOTS SHOWING DIAGEOTROPISM. (Fig. 2).

Number	Nature of Area	Reaction Above Turn	Reaction Below Turn
32	even flat	neutral	neutral
7	even flat	neutral	sp. alk. 10+
7	even flat	sp. alk. 10+	sp. alk. 10+
4	even flat	sp. acid. 10+	sp. acid. 10+
12	even flat	sp. acid. 30+	sp. acid. 30+
6	even flat	sp. acid. 100+	sp. acid. 100+
7	irregular flat	neutral	sp. acid. 30+
6	slope	neutral	sp. acid. 3+

Of the eighty-one roots that showed diageotropism, seventy-five grew on poorly drained flats and six on a slope. Of these seventy-five, sixty-eight grew on even flats (nine areas) and seven on an irregular flat. The slope on which the six roots grew was the extreme base of a steeper slope, and hence almost a flat. Therefore, the water table was not far from the surface.

III. ROOTS SHOWING LESS PRONOUNCED DIAGEOTROPISM. (Fig. 3).

Number	Nature of Area	Reaction Above Turn	Reaction Below Turn
10	even flat	neutral	neutral
1	even flat	neutral	sp. alk. 3—
4	even flat	sp. alk. 10+	sp. alk. 10+
5	even flat	sp. acid. 10+	sp. acid. 10+
5	even flat	sp. acid. 30+	sp. acid. 30+
6	even flat	sp. acid. 100+	sp. acid. 100+
3	irregular flat	neutral	sp. acid. 30+
6	gentle slope	neutral	neutral
7	gentle slope	neutral	sp. acid. 3+
9	gentle slope	neutral	sp. acid. 30+
4	steep slope	neutral	neutral

Above the turn of the roots, the conditions varied from specific alkalinity 10+ to specific acidity 100+. Below the turn, the conditions varied from specific alkalinity 10+ to specific acidity 100+. As there is such wide variation in soil reactions, it seems evident that diotropism is not due to the specific alkalinity or acidity of the soil.

Of the sixty roots that showed less pronounced diageotropism, thirty-four grew on flats and twenty-six on slopes. Of these thirty-four on flats, thirty-one were found on even flats (nine areas) and three on an irregular flat. Of the twenty-six on slopes, twenty-two grew on very gentle slopes (five areas) and four on a steep slope. The slopes were gentle, with the exception of one, so that in them the water tables were not far from the surface, though lower than on the flats.

Above the turn of the roots, the conditions varied from specific alkalinity 10+ to specific acidity 100+. Below the turn, the conditions varied from specific alkalinity 3+ to specific acidity 100+. Hence, as before, there is no relation between soil reaction and diageotropism.

EXPERIMENTAL GROWING OF SEEDLINGS.

From field observations on the root systems of the common everlasting, it was not possible to determine whether diageotropism of roots in poorly drained areas was due to an excess of water in the soil, to a deficiency of oxygen, or to both. The growing of seedlings under controlled conditions in the laboratory was undertaken in order to separate these two factors.

It proved to be unsatisfactory to grow seedlings of the everlasting because of the extremely small size of the young plants, and also because the short period of viability made it impossible to make consecutive plantings. For this reason, a number of other plants were substituted. These were sunflower, *Helianthus annuus*, chosen because of its rapid growth and therefore short observation period; three varieties of tomato, Globe Tomato, Chalk's Early Jewel Tomato, and Trucker's Favorite Tomato, chosen because the tomato is one of the important truck crops of the undrained upland flats; and *Bidens aristosa*, a plant abundant in some of the upland flats (2).

Seedlings of these plants were grown under three conditions: I, in well-drained soil; II, in soil with excess of water; III, in soil with excess of water, into which air was introduced. In all cases the soil used showed a specific alkalinity of 10+.

I. Plants grown in well drained soil.

(Figs. 4-5.)

Seeds were planted about one inch deep in ordinary flower pots and germinating boxes which were supplied with good bottom drainage and kept only moist enough to insure germination and prevent wilting. The results were as follows:

TABLE SHOWING CHARACTER OF ROOT GROWTH IN WELL-DRAINED SOIL.

Name of plant	No. days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 1 Sunflower	4	8	6	Down, few short laterals
Pot 2 Sunflower	4	10	3	Down, almost no laterals. (Fig. 4)
Pot 3 Sunflower	4	10	5	Down, three plants: numerous long laterals; two plants: short roots and few short laterals
Pot 4 Sunflower	6	8	5	Down, numerous long laterals
Pot 5 Sunflower	6	8	4	Down, numerous long laterals
Pot 6 Sunflower	7	19	6	Down, numerous long laterals (Fig. 5)
Pot 7 Globe Tomato	13	8	6	Down; single tap; no laterals
Pot 8 Trucker's Favorite Tomato	15	34	15	Down, single tap root
Pot 9 Bidens aristosa	15	36	6	Down, fine roots
Pot 10 Chalk's Early Jewel Tomato	15	41	18	Down; long tap root, few laterals

Seventy-four plants were removed from the pots and examined. The roots of all of them showed positive geotropism, (Figs. 4-5). Of these seventy-four roots, twenty-nine were sunflowers, thirty-nine were tomatoes (6 Globe, 15 Trucker's, 18 Chalk's Early Jewel Tomatoes), and six were *Bidens aristosa*. Of the twenty-nine sunflowers, eleven had few or no laterals, (Fig. 4), while eighteen had numerous long laterals, (Fig. 5). Of the thirty-nine tomatoes, the six Globe and the fifteen Trucker's Tomatoes had single tap roots, and the eighteen Chalk's Early Jewel Tomatoes had long tap roots and few laterals; the six *Bidens aristosa* had few laterals. There was no change in soil reaction during the growth of the plants. From these results, the conclusion is drawn that plants grown in well-drained soil develop positively geotropic single tap roots with comparatively few or no laterals.

II. *Plants grown in soil with excess of water.*

(Fig. 6.)

Seeds of the same kinds as were planted in well-drained pots in Group I were planted in pots which were placed in a large pan filled with water having a constant level. Thus a high water table one and one-half inches below the soil surface was produced. Water was constantly flowing out through an overflow. The results are shown in table on following page.

Thirty-two plants were removed from the pots and examined. All the roots showed diageotropism, turning at the water level, (Fig. 6). Of these thirty-two roots, seventeen were sunflowers, twelve were tomatoes (eight Globe, two Trucker's, two Chalk's Early Jewel Tomatoes) and three were *Bidens aristosa*. The seventeen sunflowers (Fig. 6) had numerous, long laterals, while the three kinds of tomatoes and *Bidens aristosa* developed tap roots with no laterals. There was no change in soil reaction during the growth of the plants. It has been found by other workers (3) that *Helianthus* plants undergo a retardation in growth in length of their main roots when cultivated in water. In the case of the plants grown under poor drainage conditions, there are two factors involved that might have caused the roots to turn: First, excess of water, and second, lack of oxygen.

TABLE SHOWING CHARACTER OF ROOT GROWTH IN SOIL WITH EXCESS OF WATER.

Name of plant	No of days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 1 Sunflower	7	5	2	Tap root turns at right angles; numerous long laterals (Fig. 6)
Pot 2 Sunflower	7	7	3	Turn, numerous long laterals
Pot 3 Sunflower	4	10	3	Turn, numerous long laterals
Pot 4 Sunflower	6	8	2	Turn, numerous long laterals
Pot 5 Sunflower	6	8	2	Turn, long laterals
Pot 6 Sunflower	7	19	5	Turn, numerous laterals
Pot 7 Globe Tomato	13	8	8	Turn
Pot 8 Truckers Favorite Tomato	15	34	2	Turn, single tap root; no laterals
Pot 9 Bidens aristosa	20	31	3	Turn
Pot 10 Chalk's Early Jewel Tomato	15	41	2	Turn, poorly developed

III. Plants grown in soil with excess of water, into which air is introduced.

(Fig. 7.)

In order to separate the two factors which may have been responsible for the turning of the roots under poor drainage conditions, seeds were planted under high water table conditions, but air was introduced into the pots. From the air pump there was a hose leading through a paraffined cork into an air-tight bottle. From this vessel, air was conducted to

the bottom of each of two pots, by means of rubber tubing connecting with L-shaped tubes, which opened at the bottom of the pot. The open ends of the glass tubes were protected with cheese cloth. Air thus passed upwards through the soil. The two pots and the air container were placed in water and thus a high water table one and one-half inches below the soil surface was produced. The seeds were planted one and one-half inches below the top of the pot and one inch below them was the water table. Thus, the seeds were grown under poor drainage conditions, but did not lack air. The results were as follows:

TABLE SHOWING CHARACTER OF ROOT GROWTH IN SOIL WITH EXCESS WATER INTO WHICH AIR IS INTRODUCED.

Name of plant	No. of days to appear above ground	Days in soil after above ground	No. of plants examined	Character of root-growth
Pot 11 Sunflower	6	8	6	Down, long tap, numerous long laterals (Fig. 7)
Pot 12 Sunflower	6	8	5	Down, numerous long laterals
Pot 13 Sunflower	6	8	6	Down, long tap, long laterals
Pot 14 Sunflower	6	8	6	Down, three plants; long laterals; three plants; short laterals
Pot 15 Chalk's Early Jewel Tomato	18	22	6	Down, single tap, no laterals

Twenty-nine plants were removed, twenty-three of which were sunflowers, and six were Early Jewel Tomatoes. All the roots showed positive geotropism, penetrating the soil below the water level, (Fig. 7). Of the twenty-three sunflowers, twenty had long tap roots and numerous, long laterals, and three had short or no laterals. The Chalk's Early Jewel Tomatoes had single tap roots and no laterals. It has been found by other workers (3) that the rate of growth in roots of *Helianthus* was faster when atmospheric air was bubbled through a solution.

There was no change in soil reaction during the growth of the plants.

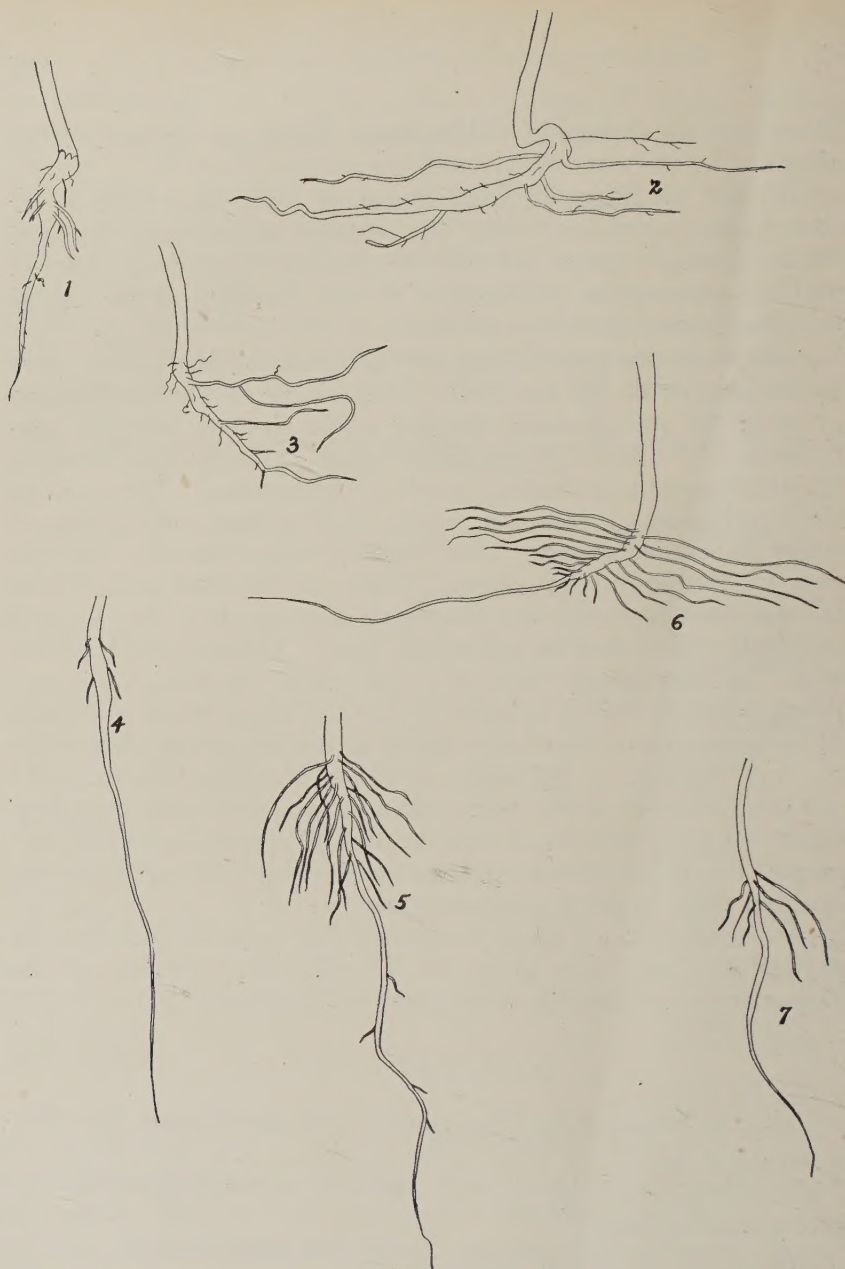
All the roots grown with excess of water and lack of air showed diageotropism; while all the roots grown with excess of water through which air was continuously bubbling showed positive geotropism. Therefore, it was the lack of air in the soil that caused the roots to turn.

The controlled conditions produced in the laboratory were similar to those in the field. The roots of the everlasting growing on well-drained, sloping areas showed positive geotropism. The roots grown under good drainage conditions in the laboratory also showed positive geotropism. The roots of the everlasting growing on poorly drained flats with excess of water in the laboratory also showed diageotropism. In the case of the roots that turned, both in the field and in the laboratory, the conditions of growth were similar. In the field the roots were found on undrained flats. The flatness, together with the fine, impervious clay soil made the flats very wet. Along with the excess of water in the soil there was a deficiency of oxygen. But it has been shown in the laboratory that when air was supplied to soil with an excess of water, the roots did not show diageotropism, but instead showed positive geotropism. Hence we conclude that it was the lack of oxygen in the soil that caused the roots of the common everlasting growing on poorly drained flats to show diageotropism.

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- Figure 1. Roots of everlasting showing positive geotropism.
 Figure 2. Roots of everlasting showing diageotropism.
 Figure 3. Roots of everlasting showing less pronounced diageotropism.
 Figures 4-5. Roots of sunflowers grown in well-drained soil show positive geotropism. Fig. 4, Sunflower showing positive geotropism and with few laterals; Fig. 5, Sunflower showing positive geotropism and with long, numerous laterals.
 Figure 6. Roots of sunflower grown in soil with excess of water show diageotropism and numerous long laterals.
 Figure 7. Roots of sunflowers grown in soil with excess of water into which air is introduced show positive geotropism.